Fossil Fruits and Seeds of the Middle Eocene Messel biota, Germany

von
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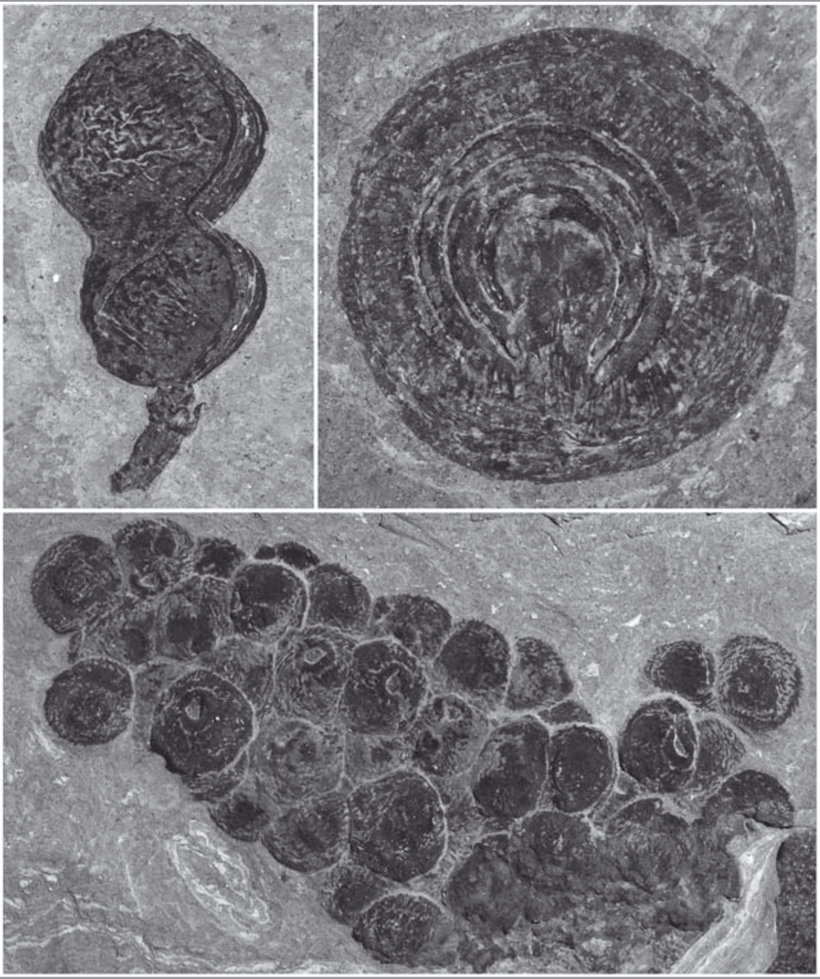

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Abstract

A survey of the extensive fruit and seed collections from the Middle Eocene (Paleogene, Tertiary) oil shale of the Messel Formation, at Messel Pit Fossil Site, a UNESCO World Heritage Site at Messel near Darmstadt, Germany, reveals at least 140 genera, representing more than 36 families. The flora includes occasional conifer remains (*Doliostrobus* scales) and numerous angiosperm remains. The following angiosperm families are represented (of which ten denoted "*" are new records for Messel): Alangiaceae (*), Altingiaceae (*), Anacardiaceae (4 genera), Apocynaceae, Arecaceae, Bignoniaceae, Burseraceae (*) (2 genera), Cannabaceae (*), Cyclanthaceae, Cyperaceae, Elaeocarpaceae (*), Euphorbiaceae, Hamamelidaceae (2 genera), Icacinaceae (6 genera), Juglandaceae (3 genera), Lauraceae (c. 4 morphotypes), Leguminosae (c. 5 morphotypes), Lythraceae, Magnoliaceae, Mastixiaceae (5 morphotypes), Menispermaceae (17 morphotypes), Myristicaceae (*), ?Nymphaeales, Nyssaceae, Pentaphylacaceae, Rhamnaceae (*), Rutaceae (5 morphotypes), Sabiaceae (*), Sapotaceae, Simaroubaceae, Tapisciaceae (*), Theaceae, Toricelliaceae (*), Ulmaceae, Vitaceae (7 morphotypes), plus 65 morphotypes of unknown familial affinity. The genera *Berchemia, Mytilaria* and *Pleiogynium* are here recorded for the first time from the Paleogene. The assemblage indicates a wide range of dispersal strategies including most modern categories of winged disseminules, pods, capsules, explosive dehiscence, a single arillate seed and two seed-types with dispersal hairs (one a coma). There is no direct evidence of epizoochory. In terms of mammalian frugivory the flora contains examples of all potential dietary categories. Tough and hard materials are abundant and soft material (e.g. in fleshy fruits) is common. Gut contents preserved in many birds and mammals prove that fruits and seeds played a part in vertebrate diets and borings in one seed type (*Rutaspermum*) indicate seed predation by weevils. No fruits or seeds show evidence of rodent gnawing. Previous quantitative studies suggesting an equable warm and humid palaeoclimate with some seasonality for Messel are supported by the newly recognised taxa. Judging from the habit of related living taxa, the vegetation appears to have been a multistratal canopy forest, including a high proportion of lianas in addition to shrubby to arborescent taxa. Herbaceous components are also present but relatively underrepresented. Among other large Eocene macrofossil floras, the Messel assemblage shows overlap with the genera known from the London Clay flora of England and the Clarno Nut Beds flora of Oregon, but relatively little similarity with floras known from eastern Asia. Compared with extant floras, the Messel flora includes a temperate component with mostly Asian endemics, and some genera that are now disjunctly distributed in the Northern Hemisphere. A large tropical-paratropical component includes genera now confined to the Old World tropics, particularly southeastern Asia and Malesia, but there are also a few exclusively Neotropical elements.

Key words: angiosperms, biogeography, flora, disseminule, exceptional preservation, frugivory, lagerstätte, liana, oil shale, palaeobotany, Paleogene, Tertiary, vegetation, vertebrate diet, aril

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Introduction

The oil shale of Messel near Darmstadt (Hessen, Germany) was discovered in the middle of the 19th century (Schaal & Schneider 1995). Soon after mining had started the first fossils were discovered. As a consequence of a number of papers by different specialists that were published in the 1920's (references in Matthess 1966, Tobien 1969), Messel became a well known Lagerstätte (Tobien 1969). All of the material was collected during mining operations until scientific excavations started in the 1960's (Kuster-Wendenburg 1969). The former oil shale mining pit of Messel is now widely known for well preserved fossils of Middle Eocene age and thus became a UNESCO World Nature Heritage Site in 1995 (Schaal 1996, 2005).

Plant fossils from Messel were initially mentioned by Chelius (1886) and later monographed by Engelhardt (1922) for the first time. The posthumously published monograph deals mainly with leaves, but includes some fruits and seeds; descriptions and comparisons were based on gross morphology and venation. As a result of a revision of old leaf material, Schweitzer (in Matthess 1966: 32f) listed seven genera in six extant families of angiosperms, but the number soon increased to 24 genera in 10 families (Sturm in Tobien 1969: 173). In an extensive study including morphological and cuticular characters Sturm (1971) later focused on leaves with affinities to Lauraceae.

As a consequence of increasing excavation activities by different institutions in the then abandoned and endangered pit, a great number of plant fossils were collected starting in the mid 1970's. Stimulated by Friedemann Schaarschmidt, the new material was studied with the application of newly developed routines for preparation using ultrasonic devices under water, storage in glycerol and imaging by various methods including epifluorescence microscopy (Schaarschmidt 1982, Ackermann et al. 1992). Following an initial note on the Messel flora by Schaarschmidt (1981), pollen and spores were monographed by Thiele-Pfeiffer (1988) and leaves by Wilde (1989). Preliminary treatments of fruits and seeds were undertaken by Collinson (1982, 1986, 1988) and flowers by Schaarschmidt (1984, 1986). Goth (1990) and Lenz et al. (2007b) described different kinds of algae by thorough SEM studies. The state of the art on the flora was summarized at different stages of knowledge on the systematic composition of the plant taphocoenosis (Schaarschmidt 1988, Wilde 2004). Important information on the Messel flora is also found in a number of papers on selected taxa and organs such as leaves of Lauraceae (Sturm 1971, Kvaček 1988), seeds of Rutaceae (Müller et al. 1985, Collinson & Gregor 1988), different remains of palms (Schaarschmidt & Wilde 1986, Harley 1997), fruits of Juglandaceae (Manchester et al. 1994), leaves of *Comptonia* L'Hér. (Myricaceae: Wilde & Frankenhäuser 2000), wood with affinities to Buxaceae (Wilde & Süss 2001), leaves and fruits of *Cedrelospermum* Saporta (Ulmaceae; Wilde & Manchester 2003), leaves of Araceae (Wilde et al. 2005), fruits of *Anacardium* L. (Manchester et al. 2007), fruits of Cyclanthaceae (Smith et al. 2008), infructescences of Cyperaceae (Smith et al. 2009b) and leaves and fruits of Malvales (Kvaček & Wilde 2010). Additional taxa were included in a methodological paper on the application of laser scanning microscopy to flowers with in-situ pollen (Wilde & Schaarschmidt 1993), in a paper on biomarkers from a mastixioid fruit containing resin (Van Aarssen et al. 1994), and in some papers comparing different localities of similar age (Wilde 1995, Wilde & Frankenhäuser 1998, Manchester 1999) and comparing this flora with other examples of exceptional preservation (Collinson et al. 2010).

Messel is the most diverse Middle Eocene fruit and seed assemblage to be documented in Europe and one of the most diverse Paleogene plant taphocoenoses worldwide. The fruit and seed flora documented here contains several new taxa, including early records of families or genera and many new morphotypes. In some cases seeds have been found in fruits and sometimes fruits are still together in infructescences. In some instances, organic attachment proves the links between different organs, e.g. leaves and fruits. Furthermore, there is the opportunity to compare the systematic diversity and composition of fruits/seeds, pollen and leaf records which have now all been studied in considerable detail (Wilde 2004).

The well preserved fruit and seed taphocoenosis of Messel also provides information on dispersal biology. Gut contents may be identified and give a direct clue to the diet of the respective animals (e.g. Schaarschmidt 1992), and specific traces of herbivory may assist in systematic assignment of the host plant (Wappler et al. 2010). Messel is important for comparison with other floras of similar age elsewhere in Europe, Asia and the New World with respect to diversity, phytogeography, climate and palaeoecology; including the reconstruction of the habitat for the insects, birds and mammals. When known in sufficient detail, evidence from the Messel fruit and seed flora may also be used for calibration of modern molecular phylogenies and for modern phytogeographic studies.

Geologic setting and age

The oil shale of Messel is the best known of about half a dozen isolated occurrences of Paleogene sediments from the Sprendlingen Horst (Harms 1999), the northernmost extension of the Odenwald structure flanking the northern part of the Upper Rhine Graben to the East. Except for Grube Prinz von Hessen, Paleogene sediments are confined to volcanogenic structures, and most are interpreted probably as maars formed by phreatomagmatic activity

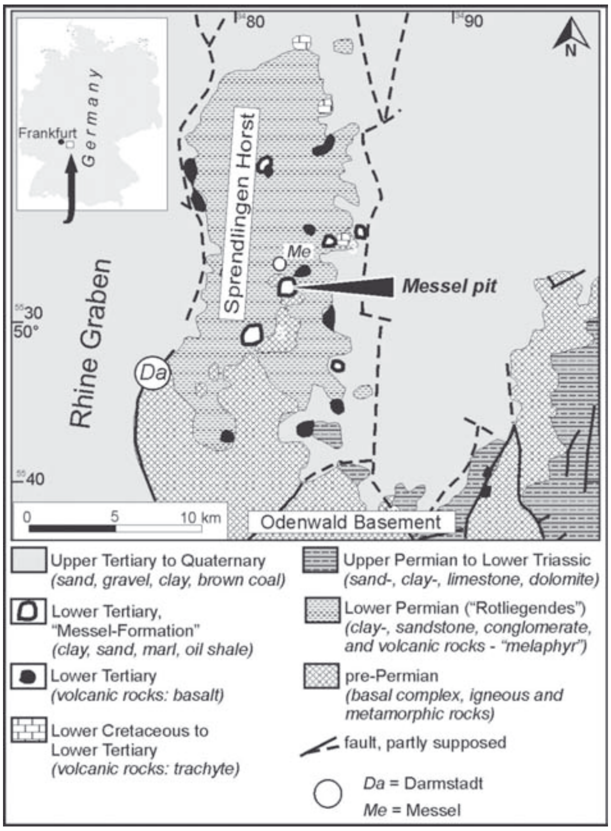


Fig. 1: Geological setting of the Messel site near Darmstadt (State of Hessen, Germany), modified from Lenz et al. 2009.

(Felder et al. 2001). The geological context of the Messel oil shale is presented in the map and stratigraphic column of figures 1 and 2. A research drilling (core Messel 2001) in the centre of the structure at Messel penetrated the lacustrine sedimentary succession of the Messel Formation into underlying volcaniclastic deposits and, finally, vent breccias. This provided definitive proof that the Middle Eocene oil shale of Messel represents deposits of a maar lake (Schulz et al. 2002, Felder & Harms 2004) which formed soon after eruption(s) ceased. The Messel Formation was initially defined by Weber & Hofmann (1982) and then subdivided by Felder & Harms (2004) with further slight modification by Lenz et al. (2007a). Sedimentation of the Lower Messel Formation started with coarse clastic debris resulting from slope failure. With increasing stability of the slopes, individual mass-flow events may be distinguished as turbidites in a background of clay and, later, even some oil shale (Felder & Harms 2004, Lenz et al. 2007a). The Middle Messel Formation, sensu Lenz et al. (2007a), includes the typical Messel oil shale as known from strata presently exposed in the pit. It was formed under permanently meromictic conditions in the lake (Irion 1977, Goth 1990). A maximum thickness of 91.5 m of the Middle Messel Formation was preserved at the site of the research core, which is equivalent to about 640,000 years as calculated from an average sedimentation rate of 0.14 mm/yr (Lenz et al. 2011). The Upper Messel Formation is not known in detail since it was largely removed by mining. As seen in recent cores through a surviving area, it includes a mixed succession of organic-rich clay, silt and sand, some lignite and most probably represents the silting-up stage of the lake and/or the marginal equivalents of the Middle Messel Formation (Matthess 1966, Felder & Harms 2004).

Except for microfossils such as pollen, spores, resistant remains of algae and sponge spicules, fossils have only been studied from excavations in an upper part of the Middle Messel Formation (c. 40 m according to Franzen et al. 1982) which was subject to mining and is still exposed in the present pit.

During early studies the biostratigraphic age of the fossil bearing oil shale at Messel was recognised as Middle Eocene by characteristic vertebrates (Haupt 1911). This was confirmed by later studies and specified as early Middle Eocene age (Tobien 1968) or lower Geiseltalian (MP 11) in the European vertebrate chronology (Franzen 2005a, b). A lower Middle Eocene age was also obtained from palynological studies (Thiele-Pfeiffer 1988; Krutzsch 1992, SPP-Zone 14/15). The core Messel 2001 finally offered the chance for radiometric dating of the underlying volcaniclastic material (47.8 million years ago (mya); Mertz & Renne 2005). We continue to use the geochronologic term "Tertiary" as appropriate according to longstanding tradition and continuing usefulness, as defined in numerous dictionaries.

Modes of preservation

The lacustrine plant taphocoenosis of the Messel oil shale is exceptional in comprising different parts and structures of plants, sometimes even in organic connection. In addition to the fruits and seeds considered here, there are leaves, pollen and spores, flowers, woody twigs and axes as well as remains of roots. Remains of angiosperms are dominant, but various conifers and pteridophytes have also been found. Algae are represented not only by resistant cysts of dinoflagellates and Zygnematales, but also by resistant sheaths and cell walls of coccal green algae like *Botryococcus* Kützing and *Tetraedron* Kützing. Remains of cell walls of *Tetraedron* are the major component of the organic material in the oil shale but are lost from palynological preparations due to their minute size (c. 4 µm diameter). Therefore, they may be recognised only by SEM (Goth 1990).

Unlike many Eocene lacustrine deposits in which the fruits are preserved as impressions, e.g. Green River, McAbee, Republic, in western North America, most of the plant fossils in the oil shale at Messel are preserved as remnants of the original organic material in various stages of compression and degradation. Although compression of the fossils in the sediment has resulted in distortion, i.e. flattening perpendicular to the pressure, the tissues and by a thick layer of small isodiametric cells (smaller than those of endocarp) with interspersed darker star-shaped sclereids, interpreted here as mesocarp.

Comments: The specimen has been broken open (uncertain whether transversely, longitudinally, or obliquely) showing circular outline, thick pericarp, and single circular locule. The inclusion of stellate-organised cells within the mesocarp, along with the internal columnar layer (pl. 21g), are diagnostic features of Lauraceae (Reid & Chandler 1933). *Laurocarpum* sp. 3 is distinguished from *Laurocarpum* species 1 and 2 by having a black outer cuticle, pericarp tissue differentiation and columnar cell layer (probable endocarp).

Specimen: SM.B Me 18005.

Lauraceae genus indet. 1
(Pl. 21c, d)

Description: Fruit globose, 4 mm in diameter, with an abruptly acute apex. Flattened by compression, preserved with a smooth dark cuticle covering through which can be seen closely spaced yellow dots.

Comments: The cuticular preservation is typical for Lauraceae. The evenly spaced yellow dots are interpreted to represent resin from oil cells which are common in Lauraceae.

Specimen: SM.B Me 8375.

Family Leguminosae Juss.

Legumes are represented at Messel by at least four different types of pods, ranging from small and single-seeded to long and multiseeded. Most are represented by only a small number of specimens and their affinity to modern legume groups is difficult to evaluate. It is likely that these represent fruits produced by the same plants as leaves and leaflets also preserved at Messel, among which five species have been recognised (Wilde 1989).

Genus ***Mimosites*** Bowerbank
Mimosites spiegeli Engelhardt
(Pl. 23a–f)

1922 *Mimosites spiegeli* Engelhardt, Abh. hess. geol. Landesanst. Darmstadt, **7** (4): 118, pl. 39, fig. 1.

Emended description: Pod stipitate (stipe up to 3.8 mm), one small calyx lobe observed (SM.B Me 19035, pl. 23c), peduncle up to 18 mm long. Pod elongate, usually curved (e.g. SM.B Me 7056, pl. 23b; 19035, pl. 23c), relatively thin (not woody), 6.0–11.2 cm long, 1.4–1.8 cm wide. Lateral margins parallel without constrictions, tapering abruptly at the apex and base. Base slightly asymmetric, acute to rounded, apex rounded. Both margins slightly thickened with the one on the placental side slightly thicker than on the other. Seed chambers 7–18, rectangular (6–8 mm × 14–16 mm), elongate across width of pod, well delimited by transverse ridges about 1 mm thick. Seed outline ovate. Seed outlines filling the width of the chambers, but usually extending only approximately 2/3 the distance towards the non-placental margin, seed outlines sometimes entirely filling the chamber (SM.B Me 19098). Venation seen only in a very small part of SM.B Me 4884, coarse veins reach to centre of pod from the placental margin, branch singly and obliquely into short lateral veins of almost equal stature. A fine reticulum is evident over the centre of the pod.

Comments: This species is readily distinguished from the other types of pods from Messel by its longitudinal curve, seeds oriented perpendicular to long axis of pod and by prominent transverse partitions delimiting the seed chambers. Specimen SM.B Me 19352 has less prominent chamber partitions than other specimens. We reillustrate here the type specimen of *Mimosites spiegeli* Engelhardt (pl. 23a). The species is now represented by many specimens in the Messel collections. As stated in the original description by Engelhardt (1922), the species is similar in pod size, morphology, and chamber delimitation to *Mimosites browniana* Bowerbank from the London Clay locality of Assington, Suffolk, England. Reid & Chandler (1933) reexamined the holotype of *M. browniana*, and noted that it was no longer possible to see finer details of structure and that therefore, they could offer “no opinion as to the generic relationship of the fruit” although Bowerbank’s original diagnosis stated “fruits which belong to the natural order Mimoseae.” Bowerbank’s specimen from the London Clay is refigured here (pl. 24h) for comparison. Although *M. spiegeli* could indeed be a mimosoid legume, there are few diagnostic characters that help to narrow down its affinities. Several species of *Albizia,* for example, have fruits that are similar in gross morphology (P. Herendeen, pers. comm., 2011).

Specimens: Holotype HLMD-Me-1760. Other specimens SM.B Me 4014, 4671, 4884, ?4885, 7036, 7056, 7057, 7067, 7072, 7162, 19035, 19098, 19352, 19353, 20054.

Genus ***Leguminocarpon*** Goeppert
Leguminocarpon herendeenii sp. n.
(Pl. 24a–d)

Diagnosis: Fruit stipitate, 1–2-seeded specimens, 14 mm long and 13.5 mm wide; multi-seeded specimen 19.5 mm long and 10.5 mm wide (excluding stipe); pedicel 3.7 mm, stipe up to 4.2 mm long. Calyx persistent with at least three lobes visible, Fruits relatively thick, asymmetrical, subcircular in single-seeded to oblong in multiple-seeded specimens, bounded by veins on both sides. Margins thickened around the periphery, one with a

Specimen: SM.B Me 8333.

Family Simaroubaceae DC.
Genus ***Ailanthus*** Desf.
Ailanthus confucii Unger
(Pl. 38l, m)

1850 *Ailanthus confucii* Unger, Denkschr. Kaiserl. Akad. Wiss Wien, Math.-Naturwiss. Cl., **1**: 23 [1850c].
1859 Heer (first picture of Unger's original specimen), Flora tertiaria Helvetiae. Vol. 3. J. Wurster, Winterthur 87, pl. 127, fig. 36.

Further synonymy provided by Corbett & Manchester (2004).

Description: Fruit biwinged, elongate elliptical, tapered at both base and apex, with a central seed. Fruit 14, 17.5, 24.5 mm long, 3, 3.7, 5 mm wide, seed elliptical, 2–4 mm in diameter. Fine, subparallel veins extending longitudinally. For detailed description see Corbett & Manchester (2004).

Comments: The Messel specimens belong to a widespread morphospecies which is also known from North America and Asia (Corbett & Manchester 2004). Although the majority of specimens in Messel are relatively small in size (less than 15 mm in length) compared to most specimens from other floras, a single specimen (SM.B Me 21808, pl. 38m) with a length of 25 mm indicates that the population from Messel is consistent with the range of dimensions normally covered by the species. Comparisons with the extant species by Corbett & Manchester (2004) indicate the closest similarity with *A. altissima* of China.

Specimens: SM.B Me 4006, 4232, 4233, 4747, 4785, 4786, 16837, 21808, 23395, 24010.

Family Tapisciaceae Takht.
Genus ***Tapiscia*** Oliv.
Tapiscia pusilla (Reid & Chandler) Mai
(Pl. 39a–l)

Basionym: 1933 *Palmospermum pusillum* Reid & Chandler, London Clay Flora 115, pl. 1, fig. 32–34.
Synonymy: 1976 *Tapiscia pusilla* (Reid & Chandler) Mai, Abh. Zentr. Geol. Inst., **26**: 122

Description: Fruit subglobose to pyriform, length 5.8–8.5 mm, width 5.0–7.0 mm, diameter 1.0–1.5 mm, bilaterally symmetrical, rounded distally, the opposite end tapering (marking the pedicel of the fruit and the micropyle of the enclosed seed). Dorsal side rounded, ventral side with a prominent obovate to triangular concavity (representing the chalazal scar beneath). Surface of pericarp with small regularly spaced scabrae, verrucae or short rugulae. Longitudinal strands linking between the ventral depression and the micropylar protrusion (representing the underlying position of the raphe).

Comments: These specimens conform to *Tapiscia* based on size and the characteristic ornamentation corresponding precisely to the single extant species, *T. sinensis* Oliv. The presence of this genus in the European Tertiary was first recognised by Mai (1976, 1980). Relatively few Messel specimens are oriented in a plane revealing the critical diagnostic characters of *Tapiscia* which are visible only on the ventral surface (e.g. pl. 39a–d, g). However, SRXTM was applied to a specimen still buried in shale with only its dorsal surface exposed (pl. 39i). The distinctive chalazal depression, micropylar protrusion, and thin pericarp over a smooth seed, are clearly seen in the resulting digital sections (pl. 39j–l). Another specimen was physically removed from the shale to reveal both ventral and dorsal surfaces (pl. 39g, h). The Messel specimens correspond in morphology and ornamentation to the species *T. pusilla* (Reid & Chandler) Mai from the London Clay. Seed moulds that could represent the same species were described as *T. subglobosa* Mai (Mai 1976, 1980) from the Middle Eocene of the Geiseltal, however as the external characters of the Geiseltal specimens are unknown, we hesitate to combine the species. The North American Middle Eocene species *T. occidentalis* Manchester (Manchester 1988, 1994) is virtually identical in morphology to this species, differing only by its smaller size. Although preserved as compressions, Messel specimens are not dried and therefore are inferred to have retained their original size.

Some specimens show large aggregations of these seeds (SM.B Me 8735; 24289, pl. 39e), without intervening tissue, or pedicels, suggesting coprolite association. One of the fruit specimens (SM.B Me 17741) appears to be attached to a very swollen peduncle (cuticle preserved and folded), but no perianth scar is present (pl. 39f). If this represents a pedicel it is more inflated than in the extant species.

Specimens: SM.B Me 2189, 2246, 2276, 2530, 4167, 4176, 4191, 4194, 4431, 4601, 8735, 12234, 12243, 13060, 13876, 14862, 14875, 14876, 14833, 16874, 17741, 18136, 18142, 18144, 19502, 21386, 24289. Other specimens are likely to exist in the collections but, as explained above, if the ventral surface is not exposed the ornamentation and size can only be taken as tentative indications of affinity.

Family Theaceae Mirb.
Genus ***Camelliacarpoidea*** gen. n.
Camelliacarpoidea messelensis sp. n.
(Pl. 40a–i)

Diagnosis: Fruit subglobose, fruit body height and width 16.5 mm, as preserved, finely rugulate, apparently leathery, flattened by compression. Apex missing, stylar condition unknown. Fruit containing at least two brittle, cracked, crushed elongate seeds, with a shiny seed coat.

Vitaceae, the seed coat (pl. 44g, i, l, m) is thicker than in any known seeds of extant genera of the Vitaceae. *Palaeovitis* from the London Clay flora and Messel have a similarly thick seed coat, but other features of morphology, like shorter ventral infolds, clearly distinguish *Crassivitisemen* from *Palaeovitis*. Most genera of Vitaceae have four or more seeds per fruit, unlike the single-seeded fruit of *Crassivitisemen*. Among extant genera of the Vitaceae, only *Cissus* L., and *Clematicissus* Planch. are regularly single-seeded (Chen & Manchester 2011). However both of these genera have an elongate chalaza that passes from the dorsal surface over the apical end of the seed, unlike this fossil which has an elongate-elliptical chalaza over the centre of the dorsal side of the seed. The composition of seed coat wall, made up of cells that are short (pl. 44m), rather than columnar, distinguishes this seed from those in the genera within the pentamerous flower clade (*Ampelocissus, Vitis, Ampelopsis, Parthenocissus,* and *Yua* C.L.Li), and suggests affinity with those with tetramerous flowers (e.g., *Tetrastigma* K.Schum., *Cayratia, Cissus, Cyphostemma* (Planch.) Alston) (Chen & Manchester 2011).

Specimens: Holotype SM.B Me 7271(as designated by Chen & Manchester 2007); paratypes SM.B Me 7371, 7552, 8205, 8786. Additional specimens: Isolated seeds SM.B Me 2354, 4806, 4937, 5735, 5750, 7969, 8394, 17509, 17532, 18896, 21423, 21429, 21495, 21579. Fruits: SM.B Me 2297, 2298, 4648, 5727, 5729-5733, 5751 (fruit with ridges of the contained seed visible at one end), 8410 (nice cross section), 8418, 23885. SRXTM was applied to SM.B Me 2298 which confirmed the seed morphology without destructive sectioning. Possible additional specimens: SM.B Me 4243, 4711, 5734.

Incertae Sedis

Genus *Carpolithus* L.
Carpolithus callosaeoides (Engelhardt) comb. n.
(Pl. 45e–l)

Description: Fruit ovate to widely ovate, massive, length 22–30 mm, width 18–25 mm, base rounded with a prominent bulging circular or almost circular scar 3–4 mm diameter, apex with a slight to marked conical depression. Surface finely longitudinally striate; striations radiating from the basal scar and converging apically. Fruit unilocular. Fruit wall thick (1.4–2 mm), composed of longitudinally elongate sclereids that are isodiametric in cross section 100–130 µm wide, with resin or latex secretions preserved in elongate strands. Resin fillings conforming to the outline of the cells. Locule usually collapsed due to compaction of the fruit, but containing a single seed (SM.B Me 2322).

Comments: We are uniting specimens that were called *Ficus callosaeoides* and *Carya costata* by Engelhardt (1922), together with more recently collected specimens. They are similar in size and share fine longitudinal surface striation, dimpled apex, thick sturdy wall, and prominent basal scar. The broken specimen (pl. 45k) shows a thick walled unilocular construction with a single seed, unlike *Ficus*. The fruit does not appear to have a plane of dehiscence or germination splitting, nor a prominent septum as would be expected in *Carya* and other Juglandaceae. The familial affinities remain uncertain, but the resin or latex material forming elongate strands as seen in the broken wall of SM.B Me 2322 (pl. 45l) may provide an important clue.

Specimens: HLMD-Me-5333 [*Carya costata* Unger sensu Engelhardt 1922: pl. 32, fig. 12], HLMD-Me-2142 [*Ficus callosaeoides* type, Engelhardt 1922: pl. 12, fig. 6a, b], SM.B Me 2321, 2322, 4098, 14093.

Genus *Saportaspermum* Meyer & Manchester
Saportaspermum kovacsiae Kvaček & Wilde
(Pl. 46a–h)

2010 *Saportaspermum kovacsiae* Kvaček & Wilde, Bull. Geosci., **85**, 112–118.

Description: Seed winged, with an elliptical seed body, subrounded and strengthened at the base and somewhat pointed at the opposite end, with a single elongate membranous wing. The rounded base of the seed shows a relatively large circular scar. Surface of seed body showing a faint longitudinal striation from alignment of surficial cells. Seed body oriented obliquely to the long axis of the wing (30–40°). One of the lateral margins of the wing is straight, the other convex, and the distal margin is rounded. Wing membranous without obvious venation, except for a vein-like thickening on the straight margin. Wing not as prominently striate as the seed body. Most of the cells on surface of the wing are polygonal and normally isodiametric, but in occasional patches the cells are slightly elongate and aligned lengthwise to the wing, but striation not visible without magnification.

Comments: There is some variability among this suite of specimens which may indicate more than one species. Similar seeds with a single elongate membranous wing occur in multiple angiosperm families, e.g. Malvaceae, Meliaceae, Proteaceae, Theaceae (Kvaček 2006). The fossil genus *Saportaspermum* is applied to seeds of this kind for which systematic affinities are unclear. The large circular scar at the rounded base of the seed (pl. 46f, h) is an additional character, seen also in the North American specimens, that may help in determining the systematic position of these seeds. This closely resembles *Saportaspermum dieteri* Walther & Kvaček from the Early Oligocene of Kundratice, Bohemia (Walther & Kvaček 2007). The Seifhennersdorf material is described as having faint reticulate venation which we do not see in the Messel specimens, and the Messel specimens have

Plate 24

Leguminosae

a–d: *Leguminocarpon herendeenii* sp. n.,

a: SM.B Me 17519, single seeded pod;

b: SM.B Me 21270, single seeded pod with subtending perianth and pedicel, apical extension suggestive of additional undeveloped seed(s);

c: holotype, SM.B Me 20422, fruit with two nearly equally developed locules and subtending perianth remains;

d: SM.B Me 18271, stipitate fruit with apical locule most developed and apparently opened apically, suggesting dehiscence;

e, f: *Leguminocarpon* sp. 1,

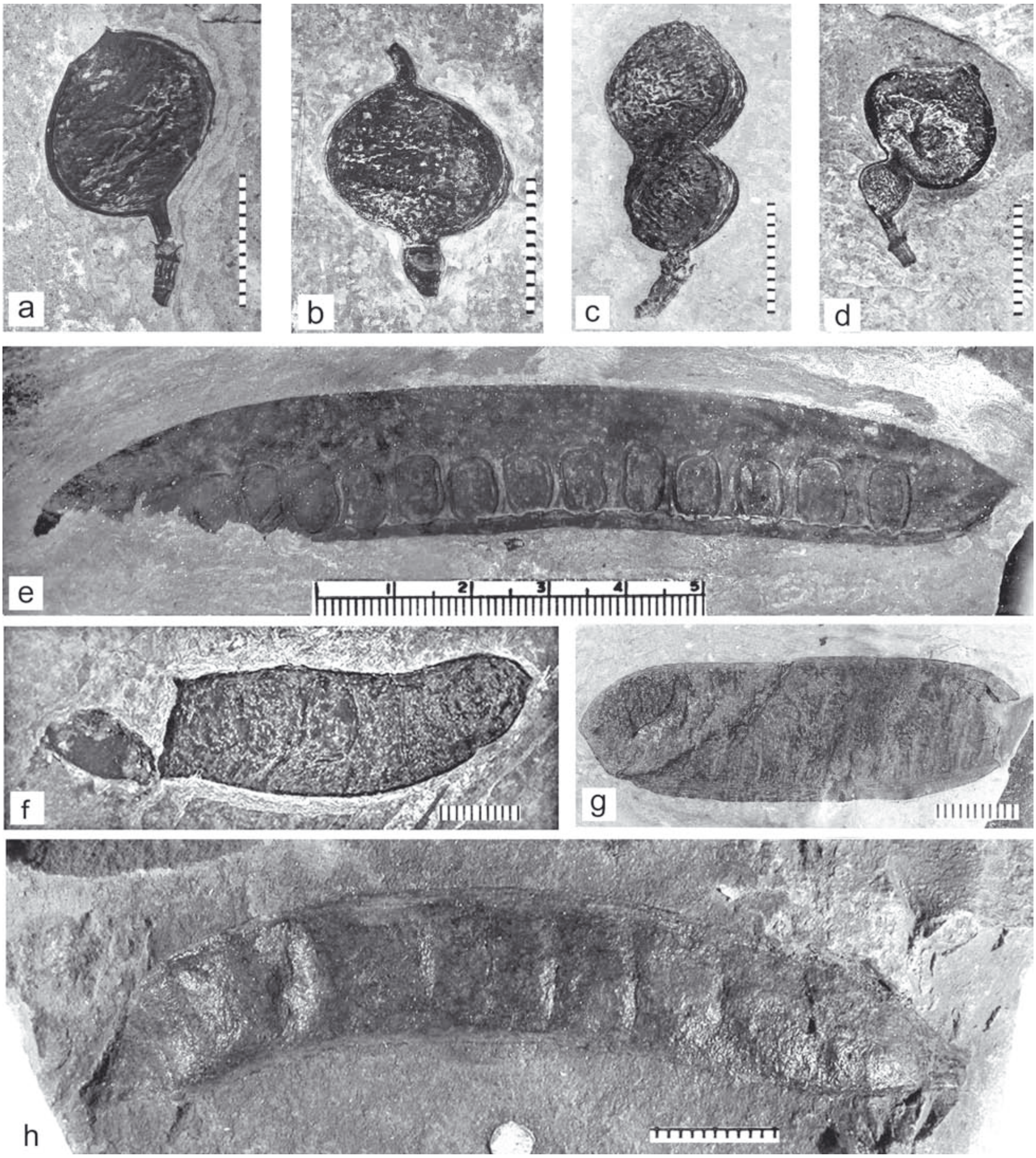
e: SM.B Me 7055, nearly straight pod, lacking transverse ridges and with seed development confined mostly to the placental side of the pod. Note rounded-rectangular seed outlines;

f: SM.B Me 7035, shorter pod with seeds of similar morphology;

g: *Leguminocarpon* sp. 2., SM.B Me 23628, pod with relatively narrow, transverse seed chambers;

h: *Mimosites browniana* Bowerbank from the London Clay (cementstone lithology), NHMUK V41174, locality of Assington, Suffolk, England for comparison with *M. spiegeli* (pl. 23);

scale bars: a–d, f–h = 1 cm; e = 5 cm.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h

Plate 25
Lythraceae

a–f: *Decodon*-like infructescences,
a, b: SM.B Me 2056;
a: paniculate infructescence;
b: enlargement of *a*, showing fruits borne on elongate peduncles and remnants of bracts/perianth;
c: SM.B Me 17917, fruits showing outlines of seeds;
d: SM.B Me 2103, pedicellate fruit with persisting single style;
e: SM.B Me 2095, single fruit with cuneiform seeds beginning to detach;
f: SM.B Me 7075, two clumps of fruits possibly deriving from a single infructescence. Some of the globose fruits on the right are transversely sectioned, showing the radial arrangement of wedge-shaped seeds;

scale bars: a, b = 1 cm; c, d, f = 5 mm; e = 3 mm.

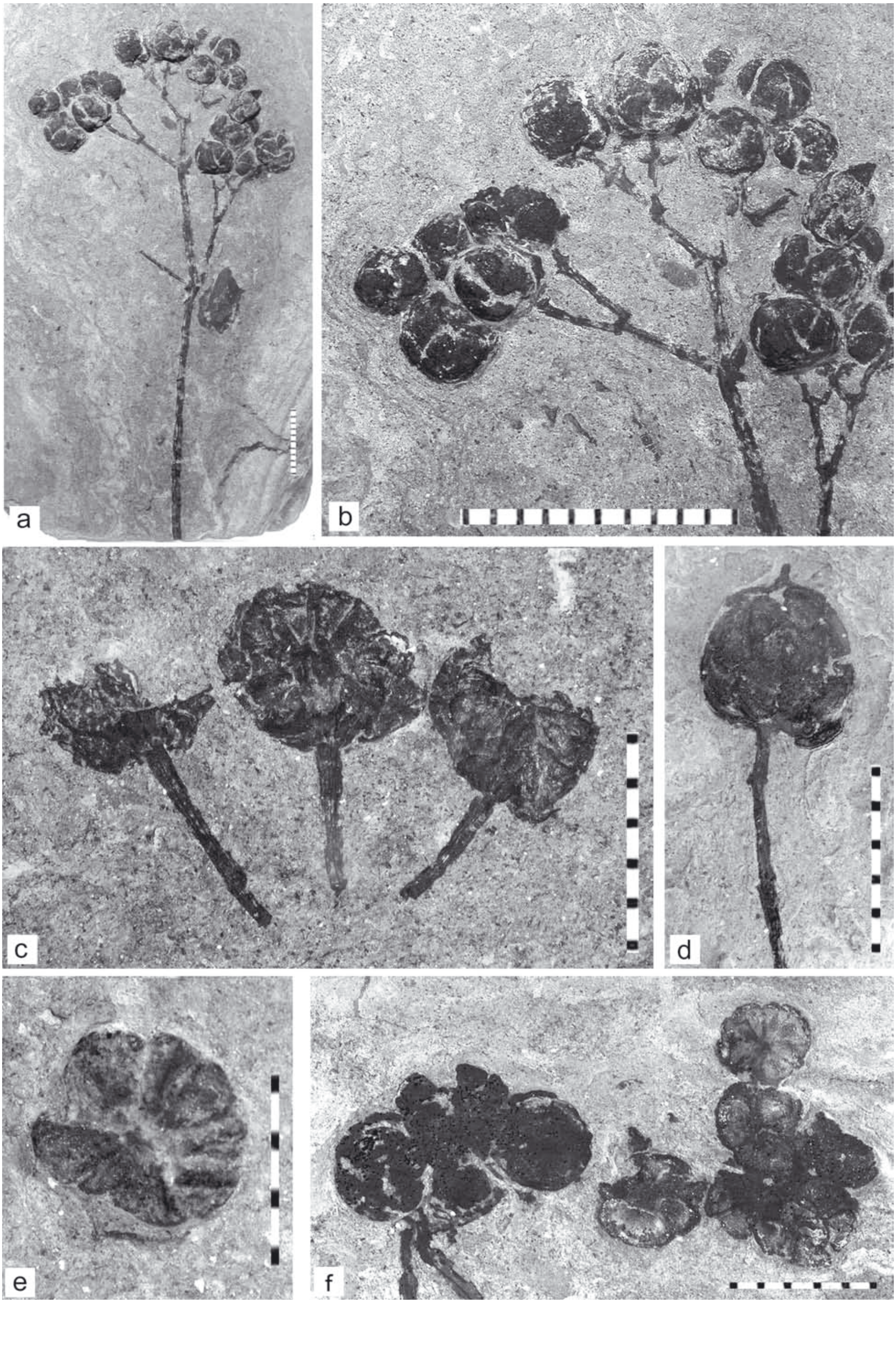
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Plate 33
Menispermaceae

a–o: *Karinschmidtia rotulae* gen. et sp. n.,

a: SM.B Me 2001, circular fruit, with pericarp outer cuticle and concentric horseshoe shaped ridges of the endocarp evident in the centre;
b: SM.B Me 7037, fruit with pericarp cuticle partially freed from sediment, casting shadow;
c, m: holotype, SM.B Me 21233, circular fruit showing radiating strands extending distally from the ridged endocarp;
d, e: SM.B Me 20452, tough radiating strands with terminal branching in the circumference, smooth central portion (concave) of endocarp;
f: SM.B Me 17153, showing cuticle sheath extending beyond the margins of the endocarp wing;
g: SM.B Me 8553, detail of fibrous strands of the endocarp wing;
h: SM.B Me 18873, isolated endocarp missing its wing;
i: SM.B Me 20543, fruit with clearly defined endocarp crests (dorsal and paired lateral);
j: SM.B 13487, fruit photographed in dry condition by reflected light;
k: specimen in *j*, photographed with low magnification epifluorescence to show cuticle;
l: specimen in *j*, under higher magnification epifluorescence, cuticle showing a polygonal pattern of epidermal cells;
m: SM.B Me 21233, enlargement from *c* showing distinct fibrous strands perpendicular to fruit margin;
n: SM.B Me 24310, basal half of a fruit showing radially striate endocarp wing and pericarp cuticle extending beyond the fibrous strands also showing the longer stylar limb and shorter hilar limb of the endocarp, the latter opposite the likely attachment position;
o: SM.B Me 24310, counterpart of *n*, apical half showing cuticle extending beyond the margin of the fibrous strands;

p–r: *Legnephora minutiflora* (K. Sch.) Diels, extant endocarp for comparison, northeastern New Guinea, Arnold Arb. Herbarium: Clemens 8682,

p: lateral view showing partially encircling winglike dorsal crest and single (rather than double) lateral crest;
q: dorsal view showing wide central area with protruding lateral crests, and narrow, wing-like median dorsal crest;
r: detail of fibrous wing-like dorsal crest by combined reflected and transmitted light;

scale bars: a–d, i–k, n, o–q = 1 cm; e–h, m, r = 5 mm; l = 150 µm.

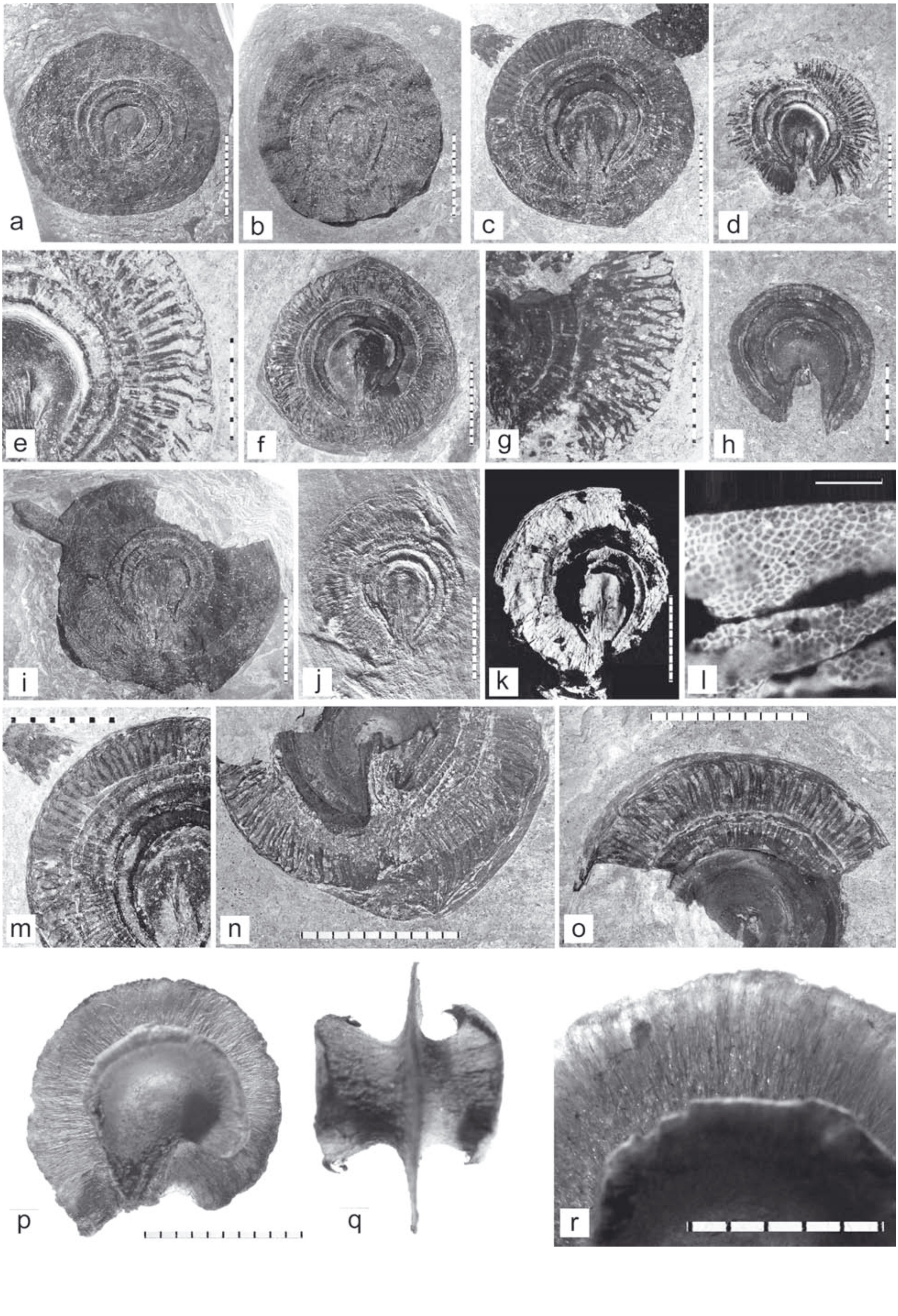
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Plate 34

Menispermaceae, Myristicaceae

a–c: *Tinomiscoidea jacquesii* sp. n.,

a: holotype, SM.B Me 2066, ventral side of endocarp showing pointed apex, median longitudinal groove and transversely to slightly obliquely oriented striae diverging from the median line;

b: SM.B Me 2068, endocarp in dorsal view, finely verrucate, with wide median and marginal ridges reflecting collapse of the dorsal wall conforming to the ventral topography;

c: SM.B Me 2067, dorsal side, showing pointed apex, rounded base, and finely verrucate surface;

d–f: *Parabaena* cf. *europaea* Czeczott & Skirgiełło,

d: SM.B Me 13741, specimen viewed dorsally with median keel transverse striate patterning, and peripheral spines;

e, f: SM.B Me 4023, another specimen showing protrusion of spines around periphery;

g, h: Tinosporeae sp. 1,

g: SM.B Me 2216, ventral surface of endocarp bisymmetrical about a median dorsal ridge, smooth;

h: SM.B Me 2218, dorsal surface of endocarp bisymmetrical about a median dorsal ridge, coarsely veruccate to rugulate;

i, j: Tinosporeae sp. 2, SM.B Me 2213. Dorsal and ventral view of smooth endocarp;

k: Unnamed Menispermaceae, SM.B Me 4091, strongly curved endocarp with three spiny crests and ridges radiating from the condylar depression (seen at right);

l–n: Tinosporeae sp. 3,

l: SM.B Me 2187, dorsal view of endocarp ruptured apically, showing sharp keel and verrucate surface;

m: SM.B Me 8830, lateral view with convex dorsal margin to left, showing verrucate surface and flattened ventral surface;

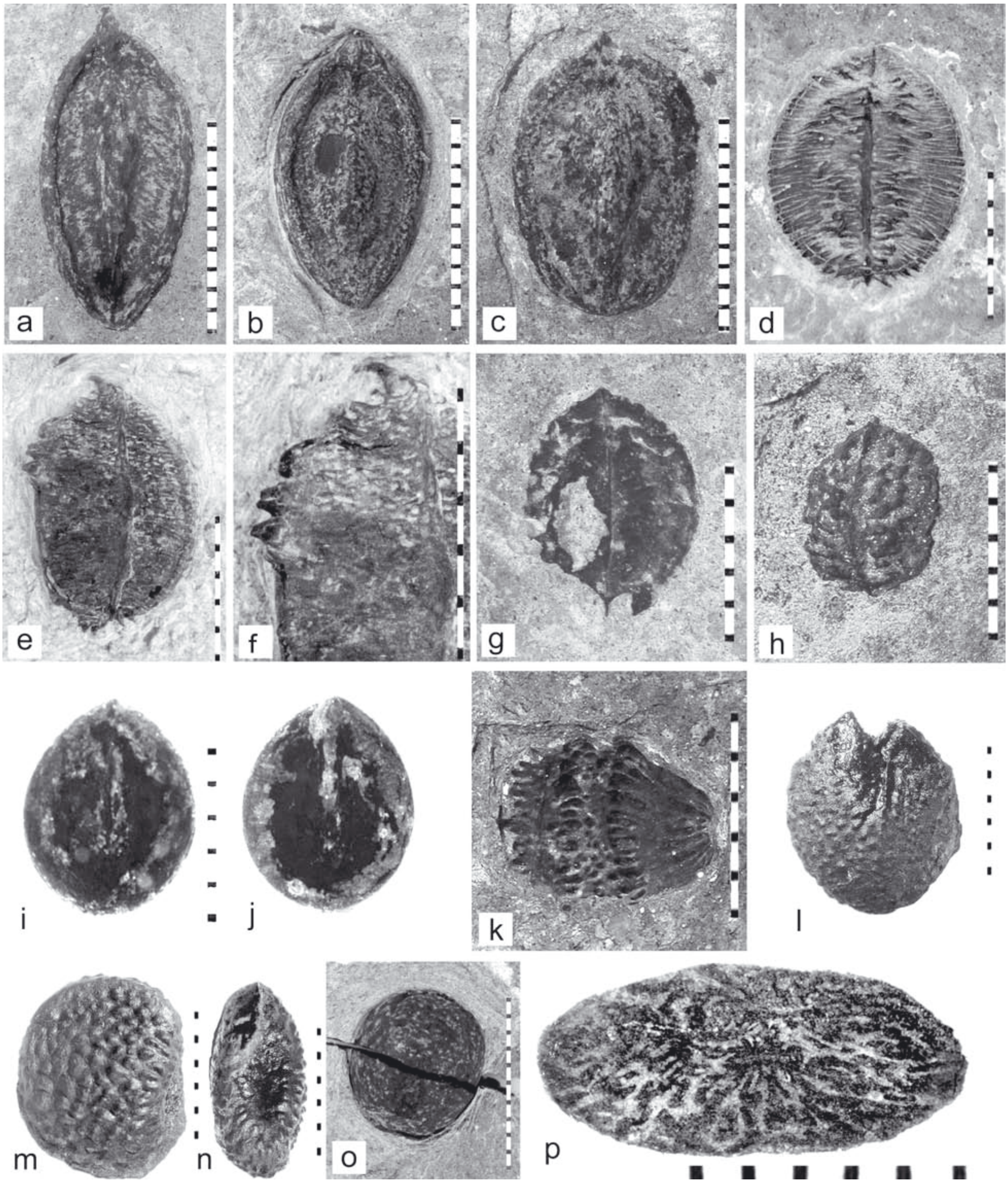
n: ventral view of *m* showing central depression and apical keel;

o, p: *Myristicacarpum* sp.,

o: SM.B Me 5605, seed circular in profile;

p: same specimen as in *o* viewed on transverse fracture plane. Ruminate endosperm with irregular longitudinal plate-like intrusions of the seed coat;

scale bars: a–c, o = 1 cm; d–n, p = 5 mm.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Taxonomic index